

Influence of Water Circulation Rate on *in situ* Measurements of Benthic Community Respiration *, **

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Abstract

The relationship between water circulation rate and benthic community respiration was investigated using *in situ* chambers fitted with variable speed pumps. A strong, positive relationship was exhibited for three estuarine study sites which represented a broad spectrum of sediment characteristics. Both aerobic respiration (65–90% of the total sediment oxygen demand, SOD) and chemical oxygen demand, COD (10–35%) increased with stirring of the overlying waters at velocities up to 20 cm s⁻¹. Contrary to the notion that COD accounts for any increase in SOD at velocities which initiate sediment resuspension, we observed that aerobic respiration was also stimulated by high velocities. We conclude that measurements of SOD in estuarine environments should be made using water circulation rates which attempt to mimic the natural environment, and that COD cannot be assumed unimportant and should be measured directly.

Introduction

The significance of water movement as a mechanism for facilitating access by benthic organisms to nutritive materials and removal of their waste products has been demonstrated for various organisms and communities including, for example, molluscs (Kerswell, 1949; Crisp, 1965; Nixon *et al.*, 1971), aquatic insects (Fox *et al.*, 1935) and algae and Aufwuchs (Odum and Hoskin, 1957; Whitford and Schumacher, 1964; McIntyre, 1966). Similarly, several authors have shown that estimates of sediment oxygen demand (SOD) may be increased with stirring of the over-

lying water (Edwards and Rolley, 1965; Carey, 1967; Martin and Bella, 1971; James, 1974; and Davies, 1975). Unfortunately, one's ability to interpret these data in relation to natural conditions is limited by the fact that the experiments have been performed typically either: with laboratory cores where mixing rate was given in relative units; or in one case (Davies, 1975) with *in situ* chambers but at only two current velocities. Smith (1978) has further cautioned against SOD measurements made under quiescent conditions because of potential problems arising from oxygen consumption by polarographic electrodes. Nevertheless, an appreciation of the importance of water circulation is apparently not universal. For example, in a review paper Pamatmat (1977) has argued that water circulation may be an important consideration only in the most vigorously mixed environments, and Hall *et al.* (1979) have even suggested that it is probably insignificant as long as sediments are not disturbed.

In most aquatic environments a portion of the observed sediment oxygen demand can be attributed to oxidation of reduced compounds arising from anaerobic metabolism (chemical oxygen demand, COD), and in some coastal areas this process may be in excess of 50% of the total oxygen demand (Jørgensen and Fenchel, 1974; Dale, 1978). Moreover, when water velocities exceed an erosion threshold, scouring of sediments can greatly increase diffusion of these reduced compounds resulting in a pulse of oxygen demand. Hence, it would seem that an inordinate amount of sediment resuspension during measurement could result in grossly exaggerated rates of oxygen uptake (c.f. Edwards and Rolley, 1965; Pamatmat, 1977). Yet sediment resuspension is a prominent feature of many aquatic environments, particularly shallow estuaries (e.g. Schubel, 1968) so that estimates of sediment oxygen demand should reflect this process.

Despite the recognized significance of benthic respiration in aquatic ecosystems, and despite the fact that these measurements are being performed with ever-increasing frequency, there is currently no consensus regarding criti-

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cal factors of design and interpretation. The purpose of this paper is to describe the relationship between mean circulation velocity of the overlying water and *in situ* measurements of sediment oxygen demand, considering such factors as sediment composition, resuspension and chemical oxygen demand. These results demonstrate the importance of water circulation on SOD and lead to suggested guidelines for design of chambers for *in situ* measurements.

Materials and Methods

This study was conducted at three sites in the Patuxent River Estuary, a tributary of Chesapeake Bay. These sites were selected to represent a wide range of sediment characteristics typically encountered along the longitudinal axis of partially-mixed, coastal-plain estuaries. Stations were located in the oligohaline, turbid zone (muddy sediments); at the lower extremity of this turbid area in the mesohaline environment (sandy-mud sediments); and at the mouth of the estuarine tributary (sand sediments). Each station was occupied for a period ranging from 1 to 7 d during July and August, 1978.

In situ measurements of sediment oxygen demand were made using two opaque Plexiglas chambers (6 mm gauge), cylindrical in shape with a circular area of 0.3 m², a height of 18 cm (12 cm above sediment surface) and an enclosed volume of 38 l. The basic design is depicted in

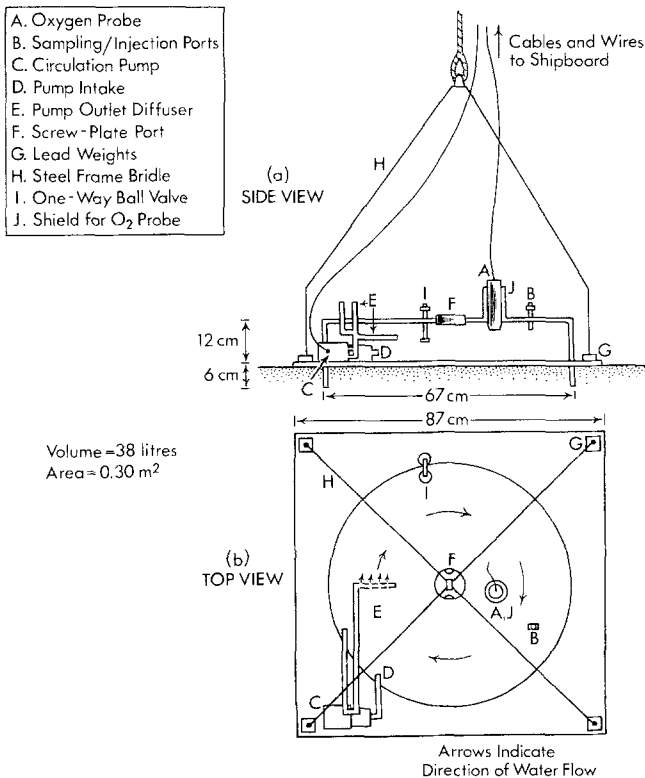


Fig. 1. Schematic diagram of experimental chamber design used for *in situ* measurements of fluxes across the sediment/water interface in estuarine environments

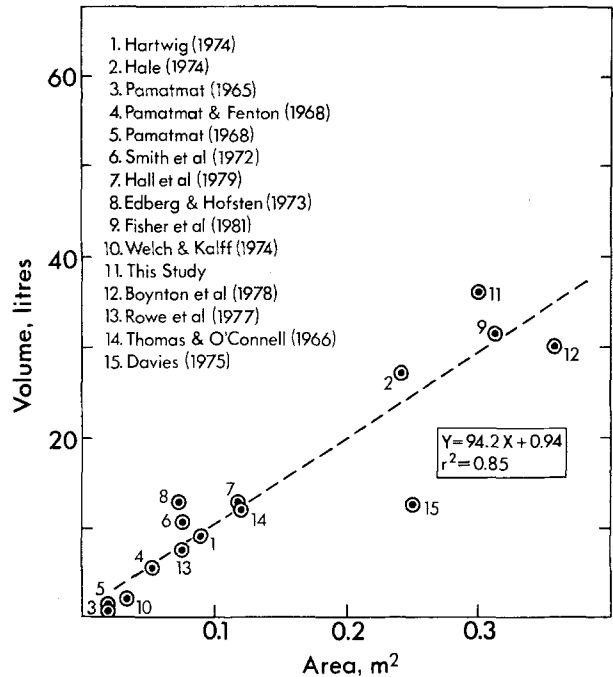


Fig. 2. Volume/area relationship for *in situ* benthic flux chambers used in various aquatic environments. Note that slope of regression line is equivalent to mean chamber height in mm

Fig. 1, illustrating several pertinent details. In an effort to examine the general applicability of our chamber design, we have plotted water volume enclosed versus sediment surface area covered for 15 chambers whose physical description was readily available (Fig. 2). It is almost uncanny that we would find a significant regression of these design data, where a coefficient of determination of $r^2 = 0.85$ was observed with a mean chamber height of about 9.4 cm. While we hesitate to make too much of this similarity, we suggest that it may provide a good starting point for those wishing to construct their own chambers. In general, greater surface area enclosed by a chamber will allow some integration of micro-habitat patchiness, while a shorter chamber height allows greater sensitivity to measure low metabolic rates. Apparently, this mean height of about 9–10 cm represents an effective balance between criteria for most aquatic environments.

The chambers were mounted on a square flange (87 cm wide) which provided a base to rest on the benthic surface, and which allowed 6 cm of the chambers' edge to penetrate the sediments, insuring proper seal. A dissolved oxygen (DO) and temperature probe (YSI 5739) was mounted in the top of each chamber. A submersible pump (Teal IP681) regulated by a rheostat (Powerstat 3PN116B) with a diffuser outlet provided reasonably uniform clockwise circulation under the chambers. Probes and pumps were connected to shipboard via cables. The pumping/circulation system was calibrated in the laboratory with the chambers inverted. Dye injection experiments allowed a visual check on the uniformity of flow, while direct current measurements using an electromagnetic induction meter (Marsh-McBirney Model 201) enabled us to calculate

mean velocities at a given rheostat setting. The circulation pattern was characterized by a near-laminar flow regime except in the mixing zone 5–8 cm out from the diffuser outlet and at the chamber's center (10–12 cm diameter) where turbulent conditions prevailed. This turbulent region was somewhat larger at higher flows, but never exceeded about 8% of the enclosed area. During pre-experiment calibration we made 40–60 discrete velocity measurements in the three-dimensional chamber volume at each rheostat setting. Actual calibrated mean velocities were slightly lower than the nominal rates but the two values never varied by more than 10%, where for instance at the nominal 10 cm s⁻¹ setting, velocities ranged from about 7.1–11.9 cm s⁻¹, with a coefficient of variation of about 15% around a mean velocity of 9.2 cm s⁻¹. Experiments were performed at nominal velocities of 5, 10, 15 and 20 cm s⁻¹. Since calibration work was done with the chambers inverted rather than on the sediment surface, we expect that current velocities inside the chambers during field experiments were somewhat slower than measured velocities and the circulation pattern somewhat more turbulent due to the frictional drag of the sediments.

During each experiment simultaneous measurements were obtained for two identical chambers placed on the bottom within about 10 m of one another. Chambers were placed in the water, voided of gases, slowly lowered to the bottom, and gently pushed (by SCUBA divers) into the sediment to the height of the flanges. After an equilibration period (15 min), the pumps were set at the desired circulation rate and turned on to initiate the experiment. Temperature and DO in both chambers were recorded at 10-min intervals for a period of about 1–3 h, during which time changes in DO ranged from about 1.5–2.0 ppm and minimum concentration never fell below 3.0 ppm. One of the chambers was then treated with formaldehyde to bring concentrations in the enclosed water to about 10% formalin. For the purposes of this paper we have followed the convention of Smith (1978), where the residual oxygen consumption after formalin treatment was defined as chemical oxygen demand. This provides at least an index of the oxidation of reduced compound diffusing from the sediments as discussed by Dale (1978). Oxygen consumption in triplicate opaque BOD bottles served as a control to account for plankton respiration.

Water samples were taken after about one hour of each incubation, both from within the chamber and from the surrounding water. These samples were then filtered through pre-weighed GFC filters and returned to the laboratory to be dried and weighed for estimating total suspended solids. At the end of each experiment, chambers were reset at a nearby location, and the entire procedure was repeated to obtain desired replication at various circulation velocities, so that a total of 82 experiments were performed in all. Temperature, salinity and sediment character, including % sand and silt/clay (obtained via sieve fractionation) and % organic carbon (as indicated by wet oxidation with potassium dichromate) were also measured at each site. On several occasions

time-series measurements were obtained for velocities in the natural environment through a full tidal cycle using a second electromagnetic induction current meter (Marsh-McBirney Model 527) held at about 10–15 cm above the sediment surface.

Results and Discussion

Sediment composition and physical characteristics of the study sites are summarized in Table 1. The silt/clay sieve fraction at the three sites spans a full range, representing 94% of the surficial (0–10 cm depth) sediment composition at the Potts Point site while only 2% at the Solomons station, with Hallowing Point being intermediate (45%). In a very approximate way, % silts and clays serves as a rough index of sedimentation rate, where an abundance of silts and clays indicates significant deposition. Similarly, organic carbon content of these sediments may suggest the net balance between organic inputs from sedimentation and consumption by the benthic community (Biggs, 1967). Again, the Potts Point sediments contained some 25 times as much organic carbon as did the Solomons sediments (2.6% compared to 0.1%), while the Hallowing Point sediments contained an intermediate level (1.0%). These data are consistent with the work of Roberts and Pierce (1976), according to which the Potts Point site lies in the middle of the estuary's turbid depositional region with Hallowing Point toward the lower end of this zone and the Solomons site in an area of negligible sedimentation. Overall, water temperatures and salinities were reasonably consistent throughout the course of this study, with temperature ranging from 24°–31°C and salinity from 5.0 to 10.5 ‰ S.

Rates of sediment oxygen demand versus mean velocity of water circulating under *in situ* chambers are pro-

Table 1. Summary of sediment and physical characteristics at the three study sites in Patuxent Estuary^a

Locations ^b	Sediment properties (% by weight)		Physical characteristics		
	Sieve Fractions ^c		Carbon Organic (%)	(°C) Tempe- rature	(‰ S) Salinity
	> 64 μ	≤ 64 μ			
Solomons	98	2	0.1	24–31	8.3–10.5
Hallowing Point	55	45	1.0	29–31	5.0–6.5
Potts Point	6	94	2.6	28–30	6.2–6.4

^a Measurements taken on the following dates in 1978: Solomons, 7–13 July; Hallowing Point, 25–27 July; Potts Point, 31 August

^b Study sites located in Patuxent River, MD. at following distances from estuary mouth: Solomons, 3 km; Hallowing Point, 37 km; Potts Point 51 km

^c Particles retained on a 64 μ mesh sieve are defined as “sands” while those passing through the sieve are termed “silts and clays”

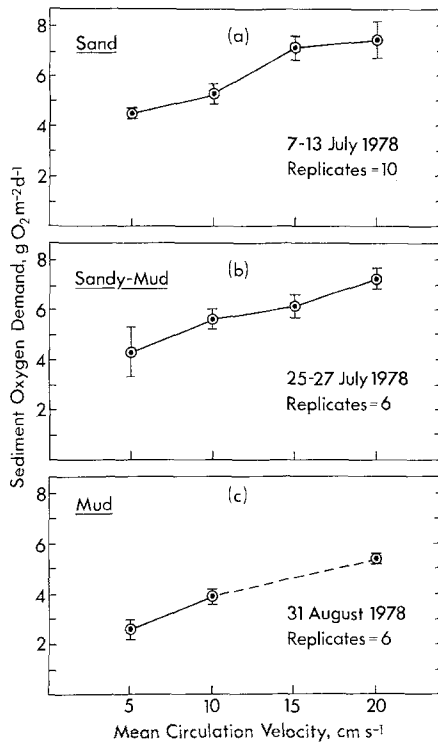


Fig. 3. Effect of water circulation rate on sediment oxygen demand (SOD) as developed from *in situ* chamber measurements in three estuarine sediments representing (a) sand, (b) sandy-mud and (c) mud environments. Sites are Solomons (a), Hallowing Point (b) and Potts Point (c)

vided in Fig. 3 for the three experimental sites. The terms sand, sandy-mud and mud are used to designate the sediment character of the Solomons, Hallowing Point and Potts Point sites, respectively. The observed values of SOD at a given circulation rate were remarkably similar at the three sites despite the extreme differences in sediment properties. For example, mean values of SOD at 5 and 20 cm s^{-1} were 4.57 and 7.41 $\text{g O}_2\text{m}^{-2}\text{d}^{-1}$ at Solomons and 4.52 and 7.01 at Hallowing Point, respectively. Measurements of SOD were somewhat lower at Potts Point, but this may be attributable to the fact that they were taken 4–5 wk later in the season. Clearly, a positive relationship exists between SOD and circulation velocity (V) at all three sites. A linear regression of these data indicates a significant ($P < 0.05$) relation at each site, where

$$\text{Sand: SOD} = 0.204 V + 3.498 \quad (r^2 = 0.752)$$

$$\text{Sandy-Mud: SOD} = 0.159 V + 3.884 \quad (r^2 = 0.643)$$

$$\text{Mud: SOD} = 0.171 V + 2.083 \quad (r^2 = 0.832).$$

However, there is an apparent non-linearity in each of these figures, and their shapes suggest certain differences which are of interest.

Using a two-way analysis of variance (SOD versus sediment type and velocity) and a Student-Newman-Kuels test of individual means, we found that at a given velocity SOD in the first two environments (sand and sandy-mud) were statistically indistinguishable. In sandy sediments

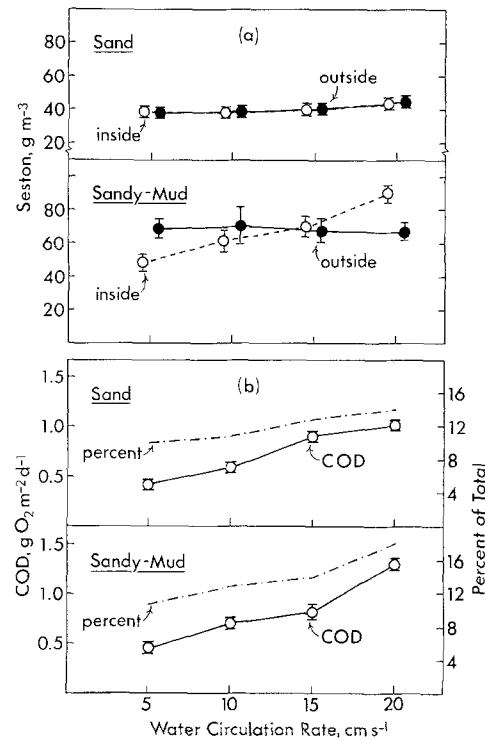


Fig. 4. Effects of water circulation rate on: (a) seston concentrations inside experimental chambers versus ambient outside conditions; and (b) chemical oxygen demand (COD) of estuarine sediments given as an absolute value and as a % of SOD. Data given for sand and sandy-mud environments

values of SOD at adjacent velocities in the experimental sequence were different only between 10 and 15 cm s^{-1} ($P < 0.05$). Apparently, the effects of increasing circulation rate were saturated beyond $V = 15 \text{ cm s}^{-1}$ where a plateau was reached. This hyperbolic relation between respiration and circulation rate has been observed previously for other heterotrophic communities (e.g. Nixon *et al.*, 1971). Similarly for the sandy-mud site, SOD was significantly different (though at a lower confidence level, $P < 0.10$) between 5 and 10 cm s^{-1} and seemed to saturate at a lower velocity (10 cm s^{-1}) than in the sandy sediments. However, between 15 and 20 cm s^{-1} the plateau appears to be disrupted, where greater SOD ($P < 0.10$) occurred at the higher velocity.

If we compare seston concentrations inside the chamber versus the open water near the sediment surface, we find distinctly different patterns for experiments performed at the sand and the sandy-mud sites (Fig. 4a). Throughout the course of the measurement sequence, seston values inside and outside the chamber were identical in the sandy environment, suggesting that experimental velocities did not resuspend or allow deposition of sediments. However, this was not the case at the sandy-mud site where seston concentrations inside the chamber were significantly lower than ambient at 5 cm s^{-1} and significantly higher at 20 cm s^{-1} . Thus, at this site the lowest of our experimental velocities appears to have been

below the critical suspension velocity (V_s) for this sediment, while the highest of our experimental velocities exceeded the erosion (or critical rolling) velocity (V_r) for this sediment. The range of velocities encountered over a tidal cycle (2–35 cm s⁻¹ at about 10–15 cm above the sediment surface) in this environment exceeds our experimental range at both ends, indicating perhaps that a marked cycle of erosion and deposition occurs here (as in other estuaries) within a single tidal period (Postma, 1967; Schubel, 1968). These velocities are well within the range of values for V_s and V_r reported for estuarine sediments (Postma, 1967; Yingst and Rhoads, 1978).

Is the observed positive relationship between circulation rate and SOD simply (as suggested by Pamatmat, 1977; Hall *et al.*, 1979 and others) the result of enhanced diffusion of reduced substances giving rise to COD? In Fig. 4b we provide measurements of COD performed contemporaneously to our SOD observations. Comparing the general shape of these COD/velocity relations to the SOD/velocity relations in Fig. 3a, b, we find a remarkable congruity, indicating that whatever the mechanism whereby circulation rate affects SOD, the same mechanism may be operative for COD. The broken line in Fig. 4b indicates that COD as a component of SOD ranged from 10–14% in sand and from 11–18% in sandy-mud, while in the muddy sediments COD approached 35% of SOD. The fraction of total oxygen demand comprised by COD roughly corresponded to the organic content in the sediments at our three experimental sites, where for instance at 10 cm s⁻¹ % COD's were 10, 13 and 30, respectively at the sand, sandy-mud, and muddy sites. Approximately 15–25% of the increase in SOD between successively increasing experimental velocities is attributable to additional COD. However, for the sandy-mud experiment where velocities presumably exceeded the critical erosion threshold and resuspension was initiated, COD accounted for some 55% of the increment in total oxygen demand. Thus, when resuspension occurred in these sediments more than half of the resulting increased sediment oxygen demand was attributable to chemical oxidation of reduced substances diffusing from these sediments.

The mechanism, by which COD is enhanced with increasing water circulation, can be explained in direct, physical terms as the results of augmented diffusion of dissolved substances between sediment interstices and open water. This process has been clearly demonstrated, particularly under conditions of sediment resuspension (e.g. Revsbech *et al.*, 1980a, b). Similarly, the enhanced biological respiration associated with increased circulation of overlying waters can be explained by increased diffusion of substrates to and end-products from the sites of biological activity. For example, at low oxygen tension (pO₂) respiration of most heterotrophic organisms will be facilitated by the increased pO₂ (Zobell and Stadler, 1940; Mangum and Van Winkle, 1973) which occurs with vigorous stirring of the water column (Revsbech *et al.*, 1980a, b). Moreover, increased water flow past sessile, suspension-feeding macrofauna expands the availability of

food which, in turn, promotes growth and metabolism of these organisms (e.g. Crisp, 1965). Hence, it is not surprising that we should find such a strong, positive relationship between water currents and both SOD and COD.

In previous studies of benthic community respiration which recognized the potential importance of water circulation effects on SOD, a prevailing view seems to have been that as long as experimental velocities are maintained below the critical erosion threshold, SOD will be primarily biological respiration, but that when resuspension occurs most of the observed oxygen demand will be COD (Edwards and Rolley, 1965; Carey, 1967; James, 1974; Davies, 1975). For instance, Davies (1975) measured SOD at circulation rates both below V_r (2–3 cm s⁻¹) and above V_r (11 cm s⁻¹), but used only the former data to estimate total annual benthic respiration. Hall *et al.* (1979) have gone so far as to suggest that “as long as sediments are undisturbed, increasing water velocity does not change the rate of oxygen exchange.” Our data suggest that this view needs to be reconsidered. We found that circulation of the overlying water does indeed enhance COD, but moreover, also increases the biological portion of SOD. On the one hand, with increasing water velocity the percent of SOD represented by chemical demand increased steadily, and when the sediment erosion velocity was exceeded, this rate of increasing percent COD rose sharply. However, the biological portion of SOD also increased sharply with incipient resuspension of sediments. There is, unfortunately, little information in the literature with which to compare our results. However, our analysis of the data of Martin and Bella (1971) indicates that in their experimental system biological respiration comprised only 49% of the total SOD in unmixed cores but more than 55% of SOD when mixing was initiated.

Thus, we would argue that circulation rates for *in situ* chambers should not be designed (as has been the case in the past) simply to maintain minimal stirring at rates well below V_r . In nature both V_s and V_r change in time and space and are influenced by biological activity of meiofauna, macrofauna and microbes (e.g. Rhoads, 1974; Rhoads *et al.*, 1977, 1978; Yingst and Rhoads, 1978). It is mistaken to think that by reducing circulation rate one can reduce COD without affecting respiration. To obtain realistic estimates of SOD, measurements should be made under conditions which simulate the hydrodynamic environment occurring in nature, recognizing that any chamber creates an environment with proximal boundaries in 6 directions rather than one, and thus the turbulent regime will be somewhat modified. We can, however, attempt to impart water velocities which approximate those typical of the system under study. That portion of SOD attributable to chemical oxidation of reduced products of anaerobic metabolism should be measured directly. The use of formalin poisoning should be considered an index of COD, and direct observation of such processes as biological and chemical sulfide oxidation are necessary to obtain more quantitative values (e.g. Jørgensen and Fenchel, 1974; Dale, 1978).

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